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Explicit experimental evidence for the role of mate guarding in minimizing loss of paternity in the Seychelles warbler

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Extra-pair copulations (EPCs) (copulations outside the pair bond) resulting in extra-pair fertilizations (EPFs) are widespread in birds. To increase reproductive success, males should not only seek EPCs, but also prevent their females from having EPFs. Male Seychelles warblers (*Acrocephalus sechellensis*) follow their partner closely during the period when these females are most receptive (fertile period). The Seychelles warbler is the first species to offer explicit experimental evidence that mate guarding functions as paternity guarding: in territories where free-living males were induced to stop mate guarding during the pair female's fertile period, the rates of intrusions by other males and successful EPCs (male mounting female) were significantly higher than those observed in the control group and in the absence of mate guarding the frequency of successful EPCs increased significantly with local male density. Male warblers do not assure their paternity through frequent copulations to devalue any sperm from other males: males do not copulate with their partners immediately following a successful EPC obtained by their partners, the frequency of successful within-pair copulations does not increase with the frequency of successful EPCs and females initiate all successful copulations and are capable of resisting copulation attempts.

Keywords: extra-pair copulation; male density; mate guarding; paternity assurance; experimentally ceased mate guarding; Seychelles warbler

1. INTRODUCTION

In many species, opportunities for males to obtain additional mates are limited (Trivers 1972). In order to increase reproductive success, males should not only seek copulations with females other than their social mate (extra-pair copulations, EPCs), but also guard their mates to prevent them from copulating with other males. EPCs resulting in extra-pair fertilizations (EPFs) are widespread in birds (e.g. Birkhead *et al.* 1990; Gibbs *et al.* 1990; Birkhead & Møller 1992; Kempenaers *et al.* 1992; Dixon *et al.* 1994; Wetton *et al.* 1995). Male birds have evolved a variety of elaborate anti-cuckoldry tactics (Birkhead *et al.* 1987) with the two most common being frequent copulation and mate guarding (Birkhead & Møller 1992). High copulation rates during the female's fertile period may function to dilute or displace any other male's sperm already present (Birkhead & Møller 1992). Mate guarding is the close following of females by their mates during the female's fertile period (starting at several days before the onset of egg laying until clutch completion), enabling the pair male to interfere with would-be cuckolders (Beecher & Beecher 1979; Birkhead 1979). Mate guarding intensity is ultimately related to the risk of extra-pair paternity, i.e. intrusion pressure from extra-pair males and female extra-pair behaviour (e.g. Alatalo *et al.* 1987; Møller 1987). Intrusions by extra-pair

males are expected to be affected by the breeding density, operational sex ratio and breeding synchrony (Westneat *et al.* 1990; Birkhead & Møller 1992). In some species with biparental care the amount of paternal care is negatively related to the proportion of extra-pair offspring (for references, see Birkhead & Møller 1992). To reduce the costs of EPCs, females are expected to engage in EPCs when they are outside the view of the pair male to mislead him about his paternity (Birkhead & Møller 1996) and when they are paired with a genetically low-quality male providing low paternal care (Kempenaers *et al.* 1992; Lifjeld *et al.* 1994).

Although mate guarding has been described for several bird species, only three male removal studies have been conducted, which showed that, in the absence of males, females obtain more EPCs (Björklund & Westman 1983; Kempenaers *et al.* 1995; Dickinson 1997; Rodrigues 1998). From previous work we also know that, when females are outside the view of their own mate, it will be easier for females to cheat him about his paternity and, hence, easier to obtain EPCs (Lifjeld & Robertson 1992; Westneat 1994). Therefore, these male removal experiments inadequately tease apart the effects of mate guarding, the costs to females of accepting EPCs (e.g. less paternal care from male partner) and female choice of EPCs. For instance, the immediate rejection of EPCs by a female would suggest there is a cost effect. We have devised an experiment allowing a finer resolution by manipulating the mate guarding activities of the male without

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removing him from the territory. In the Seychelles warbler (*Acrocephalus sechellensis*) the male abruptly ceases mate guarding from the moment he spots the single-egg clutch in the nest. By introducing a model egg into the nests of pairs during the fertile period of the female before egg laying we managed to advance this sudden switch in male behaviour, thus neutralizing his effectiveness in mate guarding without otherwise disturbing the pair bond. In this study we address the proximate and ultimate factors responsible for male mate guarding.

The entire world population of Seychelles warblers is confined to three islands: Cousin (29 ha), Cousine (26 ha) and Aride (68 ha). A salient advantage of field experiments with this species is the fact that every single adult bird is individually recognizable by means of unique leg ring combinations. Once paired, the breeding pair remains together in the same territory until the death of one member of the pair (Komdeur 1991). The level of EPFs is high (30% in 17 broods; Kappe *et al.* 1998). The fitness costs of cuckoldry are considerable because warblers usually have clutches of a single egg (91.0%, $n=223$), are single brooded with restricted breeding seasons and have no time for a successful replacement clutch (Komdeur 1996a). Both sexes feed the young equally during the four-month period of dependence (Komdeur 1991). Given the high rate of EPFs and high fitness costs of cuckoldry in the Seychelles warbler, males are expected to be under strong selection for developing efficient paternity guarding. Although Seychelles warblers breed cooperatively, in this study we used only pairs without helpers.

This study was designed to answer three questions. First, what is the influence of the female's fertile period on mate guarding and copulation behaviour? This is studied by comparing mate guarding and copulation intensity at different time intervals before and after egg laying. Second, is mate guarding efficient in lowering the EPC rate? Third, is the risk of EPCs related to the density of reproductive males? The second and third questions are tested by comparing the intrusion rates and EPC frequencies observed in warbler pairs in which some males are induced to stop mate guarding and relating this to male density.

2. MATERIAL AND METHODS

(a) *Study population and watches of focal pairs*

Seychelles warblers were studied between June and September (the main breeding period) on the island of Cousin in 1996 and 1997. All adult birds were individually colour marked and of known age and sex. We observed 21 breeding pairs to quantify mate guarding and copulatory behaviour. To control for the potential effects of age (Welling *et al.* 1995) and breeding experience (Kempnaers *et al.* 1995) on mate guarding behaviour, all focal pairs consisted of warblers between three and six years of age (during which there are no age effects on mate guarding; Komdeur 1996b) which had all successfully produced a fledgling before the onset of this study. The female's fertile period is taken as the period starting six days before egg laying until the day of laying the penultimate egg (Arvidsson 1992). In the case of the Seychelles warbler with a one-egg clutch the fertile period is assumed to last six days before the laying of the egg. All territories were checked weekly for

initiation of nest building by following females for 30 min (Komdeur 1991). During the nest building period, which lasts up to 19 days (Komdeur 1991), nests were checked daily for the presence of an egg, sometimes with the help of a mirror attached to a stick. The days of the observation period are numbered backwards from the start of laying, i.e. day -4 was four days before the first egg was laid. In this study the clutch size of all pairs was one egg. Focal pair watches started eight to 14 days before egg laying and continued until six to nine days after egg laying. The warblers are remarkably tame and easily observed. Every day, between 30 min after sunrise and 10.00 the male and female of each pair were observed simultaneously and continuously for 30 min; one observer watched the female and the other kept track of the male at the same time. For each pair we accurately determined the number of reproductive males (those over eight months; Komdeur 1996b) present in adjacent territories during the entire observation period. During the incubation period, we separated data taken when the female was off the nest from data taken while she was incubating and summed multiple watches of the same female when she was off the nest until we had 30 min of 'off-the-nest' recordings. When both members of the pair were located we recorded the following.

- (i) Foraging behaviour. We recorded whether or not foraging had taken place at 30 s intervals. The percentage foraging was expressed as the percentage of total time the warbler was seen foraging.
- (ii) Distance between pair member and birds from other territories. This was recorded as less than or greater than 5 m apart at 30 s intervals. A distance of 5 m was chosen as this is the maximum distance at which both warblers can be kept in view. If the distance was less than 5 m the birds' identity was recorded. The proximity of the male to the female was analysed as the proportion of observations that the male and female were within 5 m of each other when the female was off the nest.
- (iii) Movement initiation. We recorded as many times as possible which member of the pair initiated a movement longer than 15 m when the pair was initially in contact (within 5 m).
- (iv) Following behaviour. We recorded the proportion of following behaviour as the proportion of instances that one bird followed within 5 s when its mate flew more than 15 m from its mate. We excluded observations where the departing bird returned within 30 s, as often occurred when the female was building a nest.
- (v) Copulation solicitations, copulation attempts and successful copulations. A copulation solicitation is defined as the female dropping and shivering her wings, raising her tail in the direction of the male and giving a series of calls (Homann 1960). A copulation attempt is defined as a male trying to mount the female from above and a successful copulation as a copulation where the female allows the male to mount for a few seconds (see also Arvidsson 1992).
- (vi) Territorial or aggressive incidents between pair male, pair female and intruding birds. Whenever possible, the intruding bird's identity was recorded.

(b) *Experimentally terminated mate guarding*

We investigated the effectiveness of mate guarding in reducing the number of EPCs by inducing the male to cease mate

guarding. This was done by placing a model Seychelles warbler egg in the empty nest at the time when the female was lining the nest (one to four days before the first egg was laid). The model eggs were made of wax and painted with a waterproof marker to match the pattern of real warbler eggs. The models were placed in the nests in the early morning to mimic the laying time of real eggs and the presence-absence of the model egg and real egg was checked daily during the observation period. Females did not respond to the presence of the model egg. Immediately after the model egg was placed in the nest, the male stopped mate guarding (see §3) and began defending the egg against the egg-predating Seychelles fody (*Foudia sechellarum*), a weaver bird endemic to the Seychelles islands (Komdeur & Kats 2000). The model egg experiments were successfully conducted in 20 pairs, i.e. model eggs were 'laid' within the female's fertile period and females laid an egg in the nest which contained a model egg. In these experiments, a real egg was either laid four ($n=6$), three ($n=8$), two ($n=4$) or one ($n=2$) days after the addition of the model egg. To test the function of mate guarding as paternity guarding we only used the 14 pairs that laid their egg three or four days after the manipulation, which enabled us to calculate the variance in mate guarding intensity. To test the effect of male density on EPCs and mate guarding we used all 20 pairs. We observed females and males on the day(s) before adding the model egg and between adding the model egg and seven days after laying the real egg, using the same protocol as described above. As a control, we performed the same actions around the nests of 21 pairs, but without model egg additions.

(c) Territory quality

Seychelles warblers are insectivorous and so territory quality was expressed as the mean number of prey invertebrates available within a territory (for methods, see Komdeur 1991, 1994), because this correlated positively with adult survival and reproductive success (Komdeur 1991). The quality of all territories on Cousin was assessed monthly during the study periods in 1996 and 1997.

(d) Data analyses

Focal pair observations in 1996 and 1997 involved different pairs to avoid duplications. Observations were related to the laying of the first egg (day 0). For each variable we calculated a mean daily value across all pairs from day -14 to day 9. Because most variables deviated from normality we used non-parametric statistics for most of the analyses. In parametric tests, the proportions were angularly transformed. Unless stated otherwise, means are expressed with standard deviations, probability values are two-tailed and the null hypothesis was rejected at $p < 0.05$.

3. RESULTS

(a) Copulation behaviour

(i) Within-pair copulations and changes in female receptivity

We examined the temporal patterns of copulation to determine the female's receptive period. In total, 32 copulation attempts were recorded, of which 22 (68.8%) were successful. The rate of within-pair copulation attempts varied significantly across the female's pre-fertile, fertile and post-fertile periods (Kruskal-Wallis one-way ANOVA $H=17.86$, d.f.=2 and $p < 0.001$; figure 1a). The within-pair copulation rate was zero until

six days before egg laying, reached a peak in the four days leading up to egg laying (the mean rate during this period was 0.61 ± 0.15 copulations per hour) and was zero on the day of egg laying until at least nine days thereafter. As the females approached the laying stage, most of the copulations were successful. In fact, after day -4 all observed copulations ($n=20$) were successful. Females solicited all successful copulations. This result indicates that females reached their peak receptivity three days before laying and remained receptive until the laying of the first egg.

(ii) Territorial intrusions and extra-pair copulations

Thirty-eight territorial intrusions, all by males, were recorded from day -8 to day -2, with an intrusion rate of 0.52 per territory per hour (figure 1c). The intruding male behaved surreptitiously and was identified in most cases (86.8%); a significant proportion (90.9%) of these intrusions were made by a neighbouring territory holder ($\chi^2=28.37$, d.f.=1 and $p < 0.001$). Chasing between males was recorded during 92.1% of these intrusions, in which the territorial male successfully expelled the intruding male from his territory. The intrusion rate varied significantly across the pre-fertile, fertile and post-fertile periods ($H=10.70$, d.f.=2 and $p=0.005$; figure 1c) and peaked during the female's fertile period. Nine EPC attempts were recorded. Neighbouring territory holders were significantly more involved in these attempts than any other random male in the population (88.8%; $\chi^2=7.12$, d.f.=1 and $p=0.008$). All EPC attempts observed were during the female's fertile period, but only two EPC attempts resulted in a successful EPC (figure 1c).

In all cases of an EPC attempt, the male territory holder was not in the close proximity of his mate. However, in eight cases the pair male arrived within 30 s after an EPC attempt and expelled the intruding male from the territory. These are strong indications that the male is actually guarding the female against EPCs before she lays her egg. In the final case, the pair male did not arrive during an EPC attempt to chase the intruding male. Females were never seen in a territory other than that of their mate. Females were seen soliciting both successful EPCs and 42.8% (three out of seven) of unsuccessful EPCs.

(b) Mate guarding behaviour

(i) Intermate distance

The proximity of the male to the female increased from day -14 to day -10, remained high from day -9 to day -1, declined considerably on day 0 (when the egg was laid) and remained at that level during consecutive days (figure 1e). The male stayed significantly closer to the female during the female's fertile period than during the pre- and post-fertile periods ($H=17.75$, d.f.=2 and $p < 0.001$; figure 1e). During the two-day period before egg laying, the proportions of time spent foraging by males and females were independent of proximity (mean% foraging when mate distance < 5 m versus > 5 m: males, $84.9 \pm 6.9\%$ versus $84.2 \pm 7.7\%$ and females, $84.7 \pm 6.8\%$ versus $84.3 \pm 7.5\%$; Wilcoxon paired-sample test, males, $Z=0.17$, $n=21$ and $p=0.861$, and females, $Z=0.70$, $n=21$ and $p=0.481$).

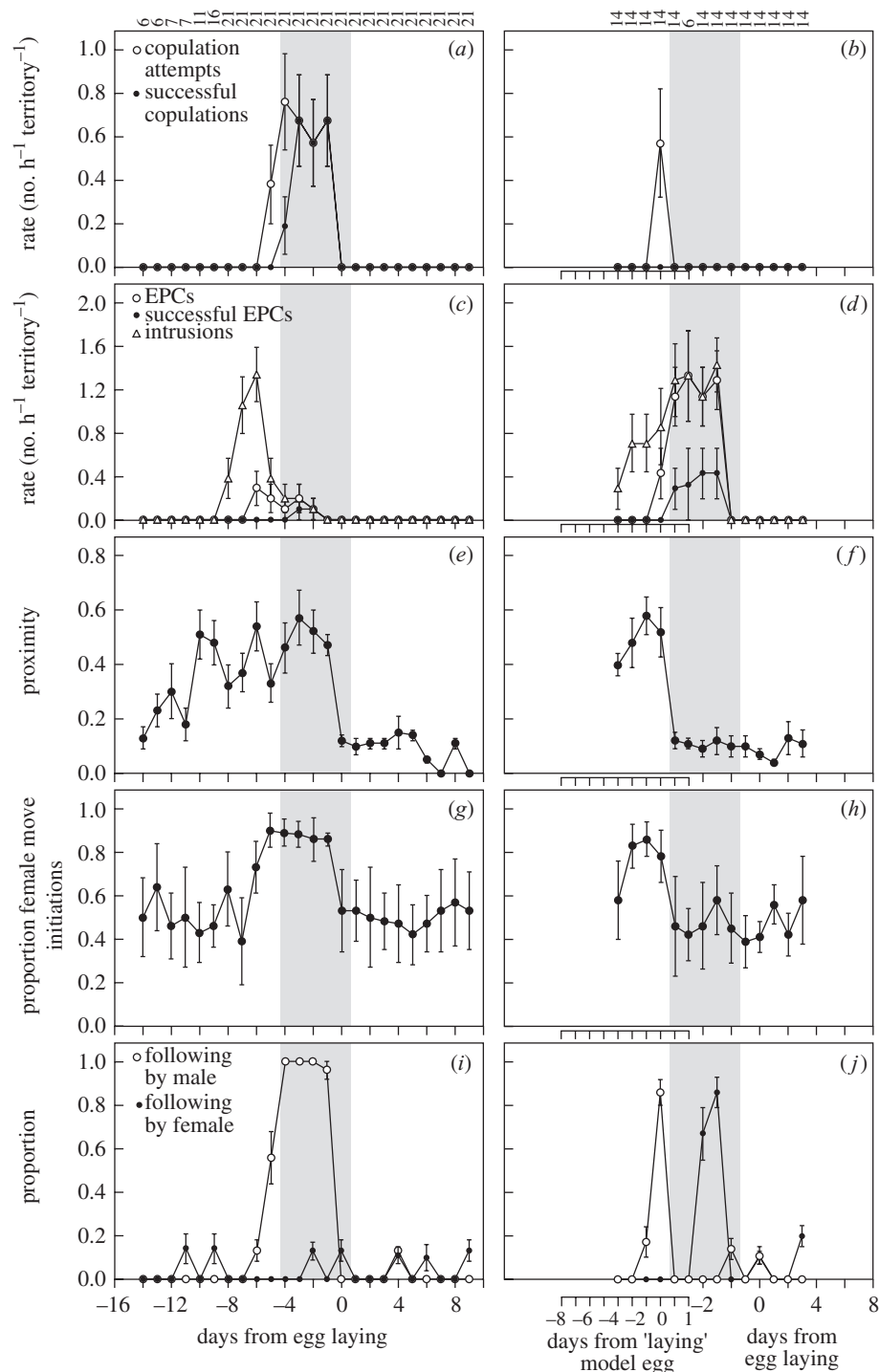


Figure 1. Temporal pattern of copulation and mate guarding behaviour in the Seychelles warbler in relation to egg laying (day 0 is the day the single egg is laid) in the control group (*a, c, e, g, i*) and in the experimental group in which males were induced to stop mate guarding (*b, d, f, h, j*). (*a, b*) Rates of male pair copulation attempts and successful copulations. (*c, d*) Rates of intrusions, EPC attempts and successful EPCs. (*e, f*) Proximity of the male to his mate. (*g, h*) Proportion of occasions females initiated a movement longer than 15 m. (*i, j*) Following behaviour by males and females. The number of observed pairs each day (30 min per pair) is indicated.

(ii) Movement initiation and following behaviour

During the female's fertile period females initiated significantly more movements than males (Wilcoxon paired-sample test, $Z=3.96$, $n=20$ and $p<0.001$), while the difference was not significant during the pre- and post-fertile periods ($Z=0.04$, $n=21$ and $p=0.964$, and $Z=0.08$, $n=16$ and $p=0.937$, respectively; figure 1*g*). During the pre-fertile period the males' tendency to

follow their mates was zero, but increased considerably and remained high during the fertile period and declined immediately to zero from the day the egg was laid ($H=19.91$, d.f.=2 and $p<0.001$; figure 1*i*). In contrast, intense mate following by females was low and did not significantly change over the course of the nest cycle ($H=2.62$, d.f.=2 and $p=0.278$; figure 1*j*). During the female's fertile period, males were more likely to follow

departing females than females were to follow departing males (Mann–Whitney U -test: $U=4.44$, $n_1=20$, $n_2=9$ and $p<0.001$). Outside this period, males and females did not differ in their propensity to follow (pre-fertile period, $U=0.57$, $n_1=15$, $n_2=17$ and $p=0.571$ and post-fertile period, $U=0.82$, $n_1=21$, $n_2=21$ and $p=0.414$). During the post-fertile period, males were observed staying close to the nest and guarding the egg when the female was not incubating the egg (Komdeur & Kats 2000). Male following behaviour was most intense (figure 1g,i) and males were closer to females (figure 1e) during the period of maximal receptivity of females to copulations (figure 1a), suggesting that males really do guard their females to enhance their paternity.

(c) *Mate guarding as paternity guarding*

We compared the frequencies of EPC attempts and successful EPCs observed in 21 control pairs and in 14 experimental pairs in which males were induced to stop mate guarding during their mate's fertile period (within three to four days after 'laying' the model egg their mates had laid an egg in the same nest). Immediately after adding the model eggs to the warbler's nests until egg laying by their mates, the proportion of movements initiated by males was significantly higher than that of control males (mean 0.51 ± 0.14 ($n=14$) versus 0.16 ± 0.26 ($n=18$) ($n \neq 21$ because both the males and females of three pairs were not observed initiating movements); $U=3.74$ and $p<0.001$; figure 1g,h). The experimental male's tendency to follow the female was zero and significantly lower than that of control males during corresponding periods (mean 0.0 ± 0.0 ($n=14$) versus 0.94 ± 0.16 ($n=18$); $U=5.38$ and $p<0.001$; figure 1i,j). Consequently, the mean proximity of experimental males to their mates was significantly lower than that of control males (mean 0.11 ± 0.04 ($n=14$) versus 0.51 ± 0.04 ($n=21$); $U=4.96$ and $p<0.001$; figure 1e,f). The proportion of male departures resulting in female following was zero from day -8 to one day after 'laying' of the model egg but, in contrast to the control group, was considerably higher from two days before egg laying to the day of laying her own egg and was zero again during the female's post-fertile period (figure 1i,j).

During the period between placing the model egg in the nests and egg laying, the experimental males stopped copulating (figure 1b) and were unresponsive to all their mate's copulation solicitations ($n=17$), whereas the control males responded to 92.9% of their mate's solicitations with a copulation ($n=28$; figure 1a). The difference in the responses to copulation solicitations between experimental and control males was significant ($\chi^2=37.39$, d.f.=1 and $p<0.001$). The rates of intrusions and successful EPCs were significantly higher when males were not mate guarding during their mate's fertile period than when the males were guarding (mean intrusions per hour 1.31 ± 0.17 ($n=14$) versus 0.12 ± 0.05 ($n=21$); $U=4.72$ and $p<0.001$; mean successful EPCs per hour 0.37 ± 0.08 ($n=14$) versus 0.05 ± 0.03 ($n=21$); $U=3.39$ and $p<0.001$; figure 1c,d). As in the control group, most intruding males in the experimental group were identified (83.9%, $n=31$); nearly all identified intrusions (88.5%) were made by a neighbouring territory holder ($\chi^2=22.38$, d.f.=1 and $p<0.001$). In all cases of intrusions into

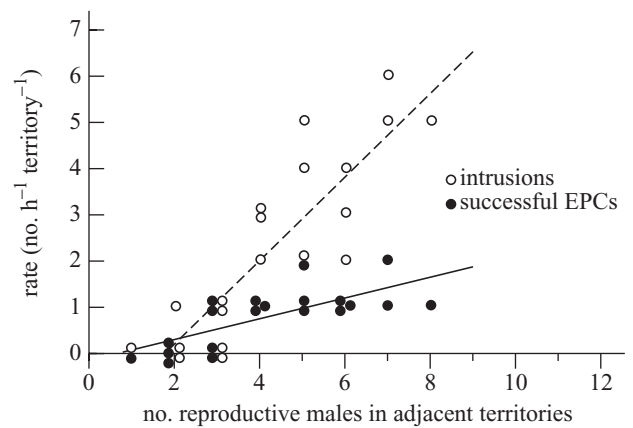


Figure 2. The influence of the number of neighbouring reproductive Seychelles warbler males (x) on the rates of intrusions and successful EPCs in territories in which males were induced to stop mate guarding during days -2 and -1 before egg laying on Cousin Island. Intrusion rate = $0.89 \times x - 1.46$ ($r^2=0.76$, $n=20$ and $p<0.001$). Rate of successful EPCs = $0.22 \times x - 0.16$ ($r^2=0.50$, $n=20$ and $p<0.001$). The quality of these territories had no effect on the intrusion rate ($r^2=0.10$ and $p=0.171$) or the rate of successful EPCs ($r^2=0.12$ and $p=0.131$).

experimental territories ($n=31$), chasing between territorial males and intruding males were not recorded.

All intrusions were by males and a significant proportion of intrusions and EPC attempts involved neighbouring males coming into the female's territory, suggesting that these neighbours are the primary threat to a male's genetic paternity. The concomitant prediction is that, in the absence of mate guarding, intrusion and EPC rates should increase with the number of neighbouring males. In territories with males that were induced to stop mate guarding during the two-day period before egg laying, the rates of intrusions and successful EPCs increased significantly with the number of neighbouring reproductive males during this period, but were independent of the quality of the experimental territories (figure 2). Of the identified intruding males and males obtaining a successful EPC, a significant proportion were from neighbouring territories rather than from any other male in the population (intrusions 84.2%, $n=38$, $\chi^2=32.70$, d.f.=1 and $p<0.001$, and successful EPCs 81.3%, $n=16$, $\chi^2=11.41$, d.f.=1 and $p<0.001$).

4. DISCUSSION

(a) *Temporal pattern of within-pair copulations, intrusions and EPCs*

Most birds copulate most frequently before laying their first egg and infrequently or not at all during egg laying (Birkhead & Møller 1992, 1993). Copulations occurring during egg laying are assumed to be inefficient for males since the uptake of sperm by the female is reduced before and after oviposition (Birkhead & Møller 1996) and unnecessary for females because they can store sperm for several days or weeks (Birkhead & Møller 1992, 1993). In the Seychelles warbler all successful within-pair copulations and EPCs (male mounts female) were initiated by the female and occurred during a short three-day period before the single egg (the entire clutch) was laid.

All territorial intrusions were by males and occurred when the focal females were in their fertile period before egg laying. In contrast to, for example, female blue tits (*Parus caeruleus*; Kempenaers *et al.* 1992), female warblers were never seen in a territory other than that of their mate. Of these intrusions 40.9% resulted in an EPC attempt and only 9.1% in a successful EPC. A significant proportion of these intrusions and EPCs involved neighbouring males. The timing of intrusions and EPCs suggests that males assess when neighbouring females are ovulating. Since warblers breed in relatively small territories (mean size 0.23 ± 0.05 ha, $n=12$; Komdeur 1991) males may easily monitor neighbouring females and obtain cues to female fertility from female behaviour during solicitation displays (dropping and shivering the wings; Hatchwell & Davies 1992) or female vocalizations. Between nest completion and egg laying, female warblers utter a series of high calls, both in the proximity and absence of their mates (J. Komdeur, personal observation). These calls were never heard outside this period and may serve as a signal of female fertility.

(b) *Mate guarding as paternity assurance*

The likelihood of EPFs is highest when females are most receptive to within-pair copulations (Birkhead & Møller 1992), leading to the prediction that paternity-assurance behaviour should be most intense during this period. Males can improve paternity through frequent copulations to devalue any sperm from other males (Birkhead 1988). This is not the case for the Seychelles warbler: (i) males do not copulate with their partners immediately following a successful EPC obtained by their partners, (ii) the rate of successful within-pair copulations does not increase with the number of neighbouring reproductive males, and (iii) females are capable of resisting copulation attempts and initiate all successful copulations. The only option to males for ensuring their paternity and reducing the need for frequent copulations is to guard their mates (that is, to follow and stay close to them), to thwart EPCs (Birkhead *et al.* 1987; Kempenaers *et al.* 1995), and to be available when their females solicit copulations (copulation access hypothesis; Gowaty & Plissner 1987). In the Seychelles warbler all EPC attempts and successful EPCs occurred when the male mate was absent. However, during most EPC attempts the pair male arrived immediately and successfully chased the intruding male away, indicating that his presence acts as a deterrent to other males. The Seychelles warbler is the first species to offer explicit experimental evidence that mate guarding by males functions as a paternity guard: (i) mate guarding (proximity and following behaviour) is extremely effective in lowering the intrusion rate and thwarting EPCs, and (ii) mate guarding intensity increases with the likelihood of being cuckolded. Such experiments in inducing free-living males to stop mate guarding during the pair female's fertile period and measuring the effect of the absence of mate guarding on females' and extra-pair males' behaviours have not been performed before (Lifjeld & Robertson 1992; Westneat 1994). However, mate guarding may also serve to protect females from harassment by other males (female-advantage hypothesis). In territories where males were made to stop mate guarding, harassment of females by other males and

the proportion of male departures resulting in female following were significantly higher than in the control group.

(c) *Cues to stop mate guarding, intruding and copulating*

Mate guarding, male intrusions and (extra-pair) copulations in the Seychelles warbler stopped completely after laying of the single-egg clutch. This is not the case in species laying more than one egg, where intrusions and copulations continue after the first egg through to the last day of laying and beyond (e.g. Alatalo *et al.* 1987; Westneat 1987; Birkhead 1988; Hobson & Sealy 1989; Arvidsson 1992; Sheldon & Burke 1994). Our model egg experiment shows that the presence of a single egg in the nest is the cue for males to stop mate guarding and copulating, despite the fact that their mates were soliciting within-pair copulations. It seems that pair males anticipate a one-egg clutch after which their partner does not need guarding, which seems feasible because the usual clutch size is a single egg. Immediately after 'laying' the egg, males are faced with a trade-off between mate guarding and guarding the egg against the egg-predating Seychelles fody (Komdeur & Kats 2000). It seems that extra-pair males use other cues, such as female vocalizations and female-initiated copulation solicitations, to value their copulations.

(d) *Sexual conflict over mate guarding*

Females may participate in EPCs to separate the choice of a genetic sire for their offspring (indirect genetic gains) from the choice of a social mate based upon territory quality or parenting ability (direct phenotypic gains) (Frederick 1987; Sherman & Morton 1988; Westneat *et al.* 1990; Gowaty & Bridges 1991). In this case mate guarding can be viewed as a conflict between the sexes, males trying to deter female EPCs and females trying to escape from his guarding to seek EPCs. Blue tit males that were in a poor condition during the pre-breeding period were often left alone by their mates who were seeking EPCs with high-quality males and had a significantly higher proportion of extra-pair young in their nest than high-quality males (Kempenaers *et al.* 1995). Unattractive blue tit males should guard their mate more intensively than attractive males. In the Seychelles warbler paternal care is important for female reproductive success (Komdeur 1991) and is negatively related to the male partner's relatedness to the offspring (Komdeur 1994). The possible reason that all EPCs occurred outside the view of pair males is to mislead the male partner as being the sole father of the offspring and to receive full paternal care. Female warblers may also benefit from mate guarding because they spend less time fending off intruding males. Whether there is a sexual conflict over mate guarding in the Seychelles warbler is currently being addressed by comparing the paternity of eggs produced by non-guarded and guarded females and by comparing the indirect (genetic) and direct (phenotypic) costs and benefits of extra-pair mating for individuals of both sexes.

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